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SPATIOTEMPORAL VARIATION IN PHENOLOGY AND ABUNDANCE OF FLORAL RESOURCES ON SHORTGRASS PRAIRIE

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ABSTRACT.— Phenology and abundance of the floral resources used by bees and other flower-visiting insects were recorded weekly from permanent quadrats for two years on two shortgrass prairie sites in the Laramie Basin, Wyoming. Each site was composed of three distinct plant communities. Results suggest considerable spatiotemporal variability in floral resources. Specifically, most species at both sites showed the following temporal variation: (1) bloom times between one and two weeks earlier in the second year; (2) differences of approximately 1–2 weeks in bloom span between years; (3) substantial differences in abundance of flowers between years. Species blooming during the last half of the census period were significantly more variable in flower abundance between years than those blooming earlier. Spatial variation was shown both by differences between sites and between plant communities within sites in the direction and magnitude of between-year changes in floral abundance. For example, floral production at Boulder Ridge in 1976 was much lower than in 1975, but at The Dirt Farm between-year differences were less pronounced and depended upon season. Similarity measures and cluster analysis suggest differences in the structure of the bloom season at both sites between years, and a relatively rapid turnover of floral composition within years such that bees face a very different flora over the latter part of their flight seasons relative to that encountered initially. Evidence from other reports support the hypothesis of spatiotemporal unpredictability of floral resources.

Spatial and temporal heterogeneity in resource supply is receiving increasing attention in ecological hypotheses concerning both species diversity and consumer foraging strategies (see reviews in Wiens 1976, Levin 1976). An important component of such resource heterogeneity is its predictability (Wiens 1976). When resources are unpredictable in time or space, generalists are hypothesized to dominate the consumer fauna because they are less vulnerable than specialists to fluctuations in the supply of particular resources (Pianka 1966, 1970, Levin 1968, Cody 1974, Moldenke 1975). Though this hypothesis is intuitively attractive, existent evidence is equivocal (Futuyma 1976, Rabenold 1978).

In addition, the resource predictability hypothesis has been extended to explain latitudinal diversity gradients by proposing that high tropical diversity is the result of close

species packing of specialists in a predictable environment (Pianka 1966, 1970). However, the assertion of large differences in predictability between temperate and tropical regions has recently been challenged by Wolda (1978), who has shown that precipitation patterns appear no less variable in the tropics and that insect populations in the seasonal tropics fluctuate as much as their temperate counterparts.

The impression that high spatiotemporal variability in resources is more common in certain regions is primarily intuitive or rests on anecdotal evidence; convincing documentation is lacking (Ricklefs 1973). Clearly, if resource predictability and spatiotemporal heterogeneity are to play more than a hypothetical role in ecology, more quantitative field studies are needed that measure changes in resource levels and their use across space and time.

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For many consumer guilds, it is difficult to distinguish between what is and what is not a resource (Haigh and Maynard Smith 1972). In contrast, flowers, the trophic resources of bees and other animals, are easy to delimit and quantify. In this report we present two years' data on variation in phenology and abundance of entomophilous flowers on two shortgrass prairie sites in SE Wyoming. Future papers will relate these data to the structure of the bee community (Tepedino and Stanton, in preparation).

The Great Plains are subject to the wide and unpredictable fluctuations in temperature and moisture availability which typify interior, temperate climates. Shortgrass prairie experiences the most unpredictable fluctuations in precipitation of all North American grassland biomes (Wiens 1974). For example, two of every five years may be expected to deviate by a minimum of 25 percent from mean yearly precipitation and one of 12 deviates by at least 50 percent; this variation is temporally unpredictable (Wiens 1974). In addition, precipitation frequently occurs in localized patches and is spatially unpredictable (Coupland 1958).

Low climatic predictability prompted the following hypotheses for flower production:

1. Floral phenology and abundance exhibit wide year-to-year variations at a given site, both at the level of the species and, more generally, for the whole community.
2. If climatic variation is spatially localized, then within-year differences between sites in floral phenology and abundance should be evident.
3. Between-year variability is modified by seasonal effects. In particular, the spring flora exhibits greater year-to-year variability than the summer flora (Leopold and Jones 1947).
4. Within-year predictability, i.e., the probability of encountering similar floral composition for several consecutive weeks, is greatest during the summer blooming season.

METHODS AND STUDY SITES

Study Sites

The study was conducted in the southern part of the Laramie Basin, a semiarid inter-

mountain valley in Albany County, Wyoming. In general, soils are shallow, rocky, and poorly developed. Precipitation in nearby Laramie averages 25.6 cm per year, with 70 percent falling from April through September. The growing season is short, varying between 80 to 100 days, with killing frosts common in June and early September. With few exceptions, the flora is composed of perennial species.

The Dirt Farm

Located approximately 16 km southeast of Laramie, The Dirt Farm site is 1.6 ha in area at an altitude of 2250 m. The vegetation is divided into three contiguous communities. A cushion plant community covers 0.77 ha and is located on windswept shallow soils with frequent bedrock exposure. Abundant species include *Phlox bryoides*, *Astragalus sericoleucus*, *A. spatulatus*, *Arenaria hookeri*, and *Paronychia sessiliflora*, all of the caespitose, herbaceous growth form. Adjoining the cushion plant community is a level area of 0.33 ha dominated by the shrub, *Cercocarpus montanus*, mountain mahogany. Associated species include *Allium textile*, *A. cernuum*, and the half-shrub *Chrysothamnus viscidiflorus*. Soils are very shallow or nonexistent here also, with the roots of the shrubs penetrating cracks in the bedrock. Extending south from the mountain mahogany community is a 0.5 ha section of typical shortgrass prairie. Soils are deeper here than in the other two communities.

Boulder Ridge

The Boulder Ridge site covers 1 ha and is located approximately 38 km southwest of Laramie (22 km southwest of The Dirt Farm) at an altitude of 2425 m. The vegetation is foothill scrub (Porter 1962) and is divided into three communities. A central section of 0.35 ha is dominated by the shrub *Cercocarpus montanus* with a few individuals of the shrubs *Prunus virginiana*, *Amelanchier alnifolia*, and *Ribes cereum*. Abundant associated herbs are *Allium textile*, *A. geyeri*, *A. cernuum*, *Ranunculus ranunculinus*, and *Cerastium arvense*. The western part of the community is level, but the eastern end

slopes at an angle of approximately 30 degrees. At slope bottom mountain mahogany gives way to a community of 0.28 ha dominated by sagebrush (*Artemisia tridentata*). The most abundant associates are *Castilleja flava*, *Astragalus flexuosus*, *Collinsia parvifolia*, *Orthocarpus luteus*, and *Chrysopsis villosa*. Bordering the study site at its eastern and western ends is a heterogeneous community of 0.37 ha that includes representatives of the cushion plant, shortgrass prairie, and sagebrush communities. Nomenclature is that of Harrington (1954), Porter (1965), and Weber (1967).

Methods

Censusing.—Floral phenology and abundance of species with entomophilous flowers were estimated for two years at each site by weekly censuses of the number of flowers by species in permanent m² quadrats. Censusing extended from the last week in May through the last week of August, except for the Boulder Ridge site in 1975, which began one week later because of a spring snow storm. Quadrats were chosen by using a stratified random sampling technique to insure that each community was sampled in proportion to its percentage of the entire study area. Approximately 1.6 percent of the total area of each site was sampled. Individual flowers were counted in all cases except for most Compositae, where heads were counted, and the Umbelliferae and Polygonaceae, where umbels were counted.

Analysis.—To avoid the assumptions of normality and homoscedasticity, non-parametric statistics were used. The Sign Test (Conover 1971) was used to test for between-year differences in total floral abundance at each site by comparing the total number of flowers in each permanent quadrat for each set of paired sampling dates (Table 1). Comparisons were made for each site as a whole and by vegetation type.

To provide a measure of the similarity between sampling dates both within and between years for each site we used the Czekanowski measure (also known as the Bray-Curtis Index: Goodall 1973) to generate similarity matrices, which were then subjected to cluster analysis. The Czekanowski Index is written

$$PS = \frac{2 \sum_{i=1}^n \min(x_i, y_i)}{\sum_{i=1}^n (x_i + y_i)}$$

where x_i and y_i are the number of flowers of species i on dates x and y .

The matrices were analyzed by single, complete, and average linkage clustering algorithms using the BMDP computer package (Dixon 1975) and the best grouping method, decided by calculating the cophenetic correlation coefficient of Sokal and Rohlf (Sneath and Sokal 1973). The average linkage method provided the best results, and only these are reported. Matrices for each site for all census date comparisons as well as separate within-site, within-year matrices were clustered. Only the four within-site, within-year clusters are reported here because we consider them most informative.

TABLE 1. Actual floral census dates and their corresponding census code numbers for each study site.

Census Code	Dirt Farm		Boulder Ridge	
	1975	1976	1975	1976
1	26 May	24 May	No census	27 May
2	2 June	31 May	5 June	3 June
3	9 June	7 June	13 June	10 June
4	16 June	16 June	20 June	18 June
5	23 June	21 June	27 June	24 June
6	30 June	28 June	4 July	1 July
7	7 July	6 July	11 July	7 July
8	14 July	12 July	18 July	18 July
9	21 July	21 July	25 July	25 July
10	28 July	28 July	31 July	31 July
11	6 August	5 August	7 August	8 August
12	13 August	11 August	14 August	14 August
13	19 August	18 August	23 August	19 August
14	26 August	28 August	29 August	28 August

Results

Precipitation and temperature.—Precipitation patterns over the two years of study were quite different (Data from weather station at Laramie Airport). Rainfall in spring and early summer 1975 was much heavier than normal (Fig. 1a), and total precipitation for the year was 6.1 percent above normal. Conversely, 1976 was a dry year with below normal rainfall for every month from March through June. July and August received greater than average rainfall, and by the end of the study precipitation was only 17.0 percent below normal for the January through August 1976 period.

In general, temperatures were warmer in 1976 (Fig. 1b). In particular 1976 was warmer from April through July, a period which was also (July excluded) much drier than normal (Fig. 1a). The frost-free period in 1975 extended from 16 June to 5 September (79 days) and in 1976 from 25 June to termination of the study (29 August) (63 days).



Fig. 1. Monthly precipitation (a) and temperature (b) records from the Laramie Airport (Brees Field): a) solid line = 1975, 1976, dashed line = normal; b) solid line = 1975, dashed line = 1976.

Species Composition.—We recorded 63 and 73 entomophilous plant species during the two years at The Dirt Farm and Boulder Ridge, respectively (Appendix A). Total flowers by species and year are also shown in Appendix A. The family Compositae was represented by the largest number of species at both sites, followed by the Cruciferae at The Dirt Farm and the Scrophulariaceae at Boulder Ridge.

Dirt Farm

Phenology.—The flowering phenology of selected species is shown in Figure 2. Phenological variation between years took two forms: differences in first bloom and in bloom span. Evidence for variability in first bloom comes from several sources. First, when total floral abundance is graphed by date for each year, it is clear that both June and August peaks were advanced in 1976 (Fig. 3). It is worthwhile to note, however, that the advancement in each peak is not due to similar responses in each vegetation type. The early peak is advanced due to responses of the cushion plant and mountain mahogany communities, and the shortgrass and mountain mahogany communities account for advances in the late peak (Fig. 3). Earlier flowering in 1976 was due to a warmer spring and summer relative to 1975.

Phenological advancement in 1976 is also seen when first bloom dates are compared by species. Analysis shows that 27 of 38 species differed by at least one week in anthesis. Eleven species were excluded because they were in bloom when censusing began, and 14 others were eliminated because they flowered in only one year. Of the 27 species that differed in phenology, 24 were earlier by an average of 10 days in 1976 ($X^2 = 16.33$, $P < 0.001$).

Are there seasonal differences between early- and late-blooming species in phenological predictability? To test this the census period was halved and species grouped according to the half in which they began blooming (Fig. 3). Twelve of 18 first-half species showed a mean difference of one week in beginning bloom, and 15 of 20 second-half species showed mean advance of 12.1 days. Species blooming during the last half of the

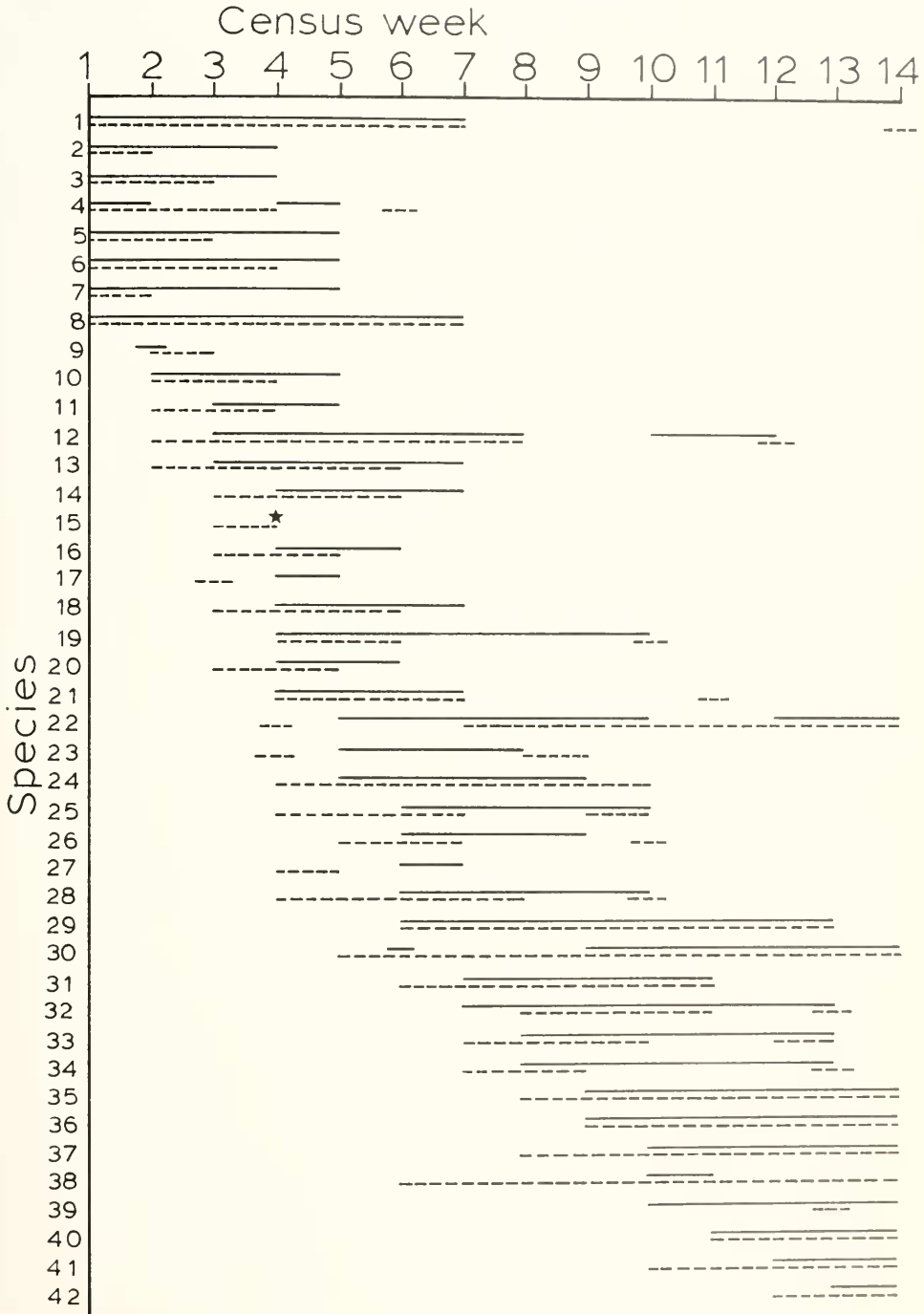


Fig. 2. Bloom spans of selected species at The Dirt Farm for 1975 (solid) and 1976 (dashed); stars = did not flow cr. Census date numbers refer to Table 1, species numbers to Appendix A.

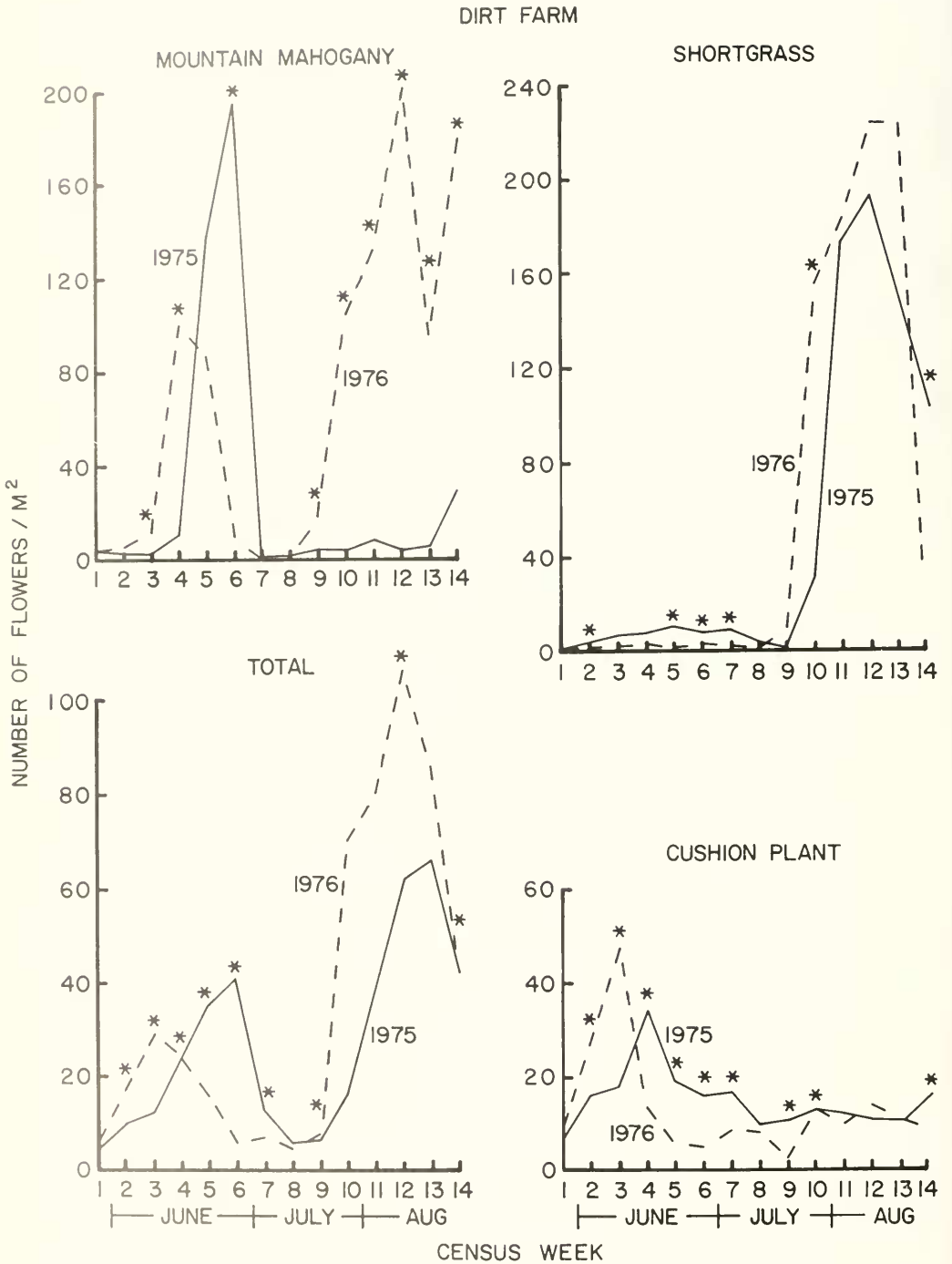


Fig. 3. Total floral abundance per m², irrespective of species, at The Dirt Farm for each census date in 1975 and 1976. Census date numbers refer to Table 1. Asterisks mark significant differences ($P \leq .05$) between years for paired dates.

season showed significantly greater phenological differences than those blooming during the first half (Mann-Whitney U-Test, $P < 0.05$).

Between-year comparisons of bloom spans are a second indicator of phenological variability. Differences of at least one week in bloom span were shown by 22 of 38 species. Average difference in bloom span for the 22 species was two weeks with a range of one to seven weeks. Ten species had longer spans in 1975 and 12 had longer spans in 1976. A comparison by seasonal grouping of bloom span data into early and later blooming species shows that longer bloom spans during the last half of the season occurred mostly in 1976, and 1975 had more longer blooming species during the first half ($X^2 = 2.76$, $P = 0.097$).

Floral Abundance.—Differences in floral abundance between years is first shown by

comparing total number of flowers by date (Fig. 3). Total abundance comparisons show the early peak to be higher but the late peak lower in 1975. The late peak difference is due largely to profuse flowering of *Eriogonum effusum*. Exclusion of this species results in much closer agreement of abundances from late July to mid-August.

When total floral abundance is partitioned into component communities it is again evident that there is no typical, overall site response (Fig. 3). For example, the mountain mahogany community shows nine significant between-year differences in abundance, with 1976 having more flowers on eight dates. In contrast, between-year differences in the cushion plant community show 1975 with more flowers for seven or nine significant comparisons and the shortgrass community with more flowers in 1975 for five of six dates. A cold period during the week begin-

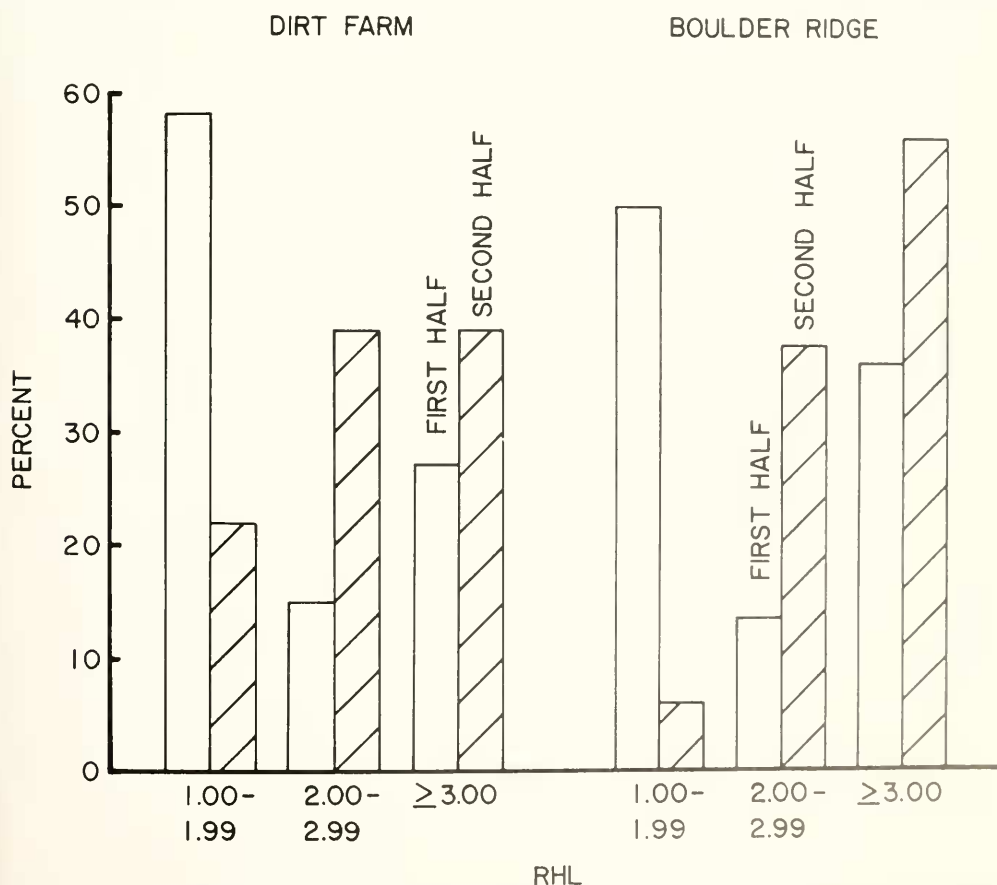


Fig. 4. Frequency distribution of the ratio of the number of flowers in the most abundant year to the number of flowers in the least abundant year for each species (*RHL*) at both sites.

ning 16 June 1976 reduced floral production appreciably on the mountain mahogany community and probably affected the shortgrass community as well. During this period temperatures were below freezing for three nights and snow and sleet fell twice. The effect of such periods upon organisms in the Rocky Mountains has been described by Ehrlich et al. (1972).

Floral abundance was also compared by species between years. An expression of differences in abundance is the ratio of total number of flowers observed in the year of highest production divided by total number of flowers in the year of lowest production (*RHL*). We eliminated from this analysis those species that either flowered in only one year or failed to produce at least 50 flowers in either year. For the remaining 44 species mean *RHL* = 5.39 (*SD* = 8.56, range = 1.04–48.60), suggesting that the abundance of flowers of most species may show significant between-year-variation. The data are shown as histograms in Figure 4. Of the 44 species, 26 were more abundant in 1975 and 18 were

more abundant in 1976. Thus, no year effect was observed.

Do *RHL* values display a seasonal pattern? Again, species were grouped according to the half of the season in which they began flowering and the Mann-Whitney U-Test used to test for differences in *RHL* between groups. The comparisons show that plants blooming during the latter half of the season were significantly more variable ($P=0.05$), i.e., had larger *RHL* values than those blooming earlier. No year effect was evident since both years had an almost equal proportion of species with highest *RHL* values in each half of the year.

Similarity and Cluster Analysis.— We used cluster analysis to elucidate differences between census dates within and between years and to illustrate seasonal groupings. High similarity values for paired between-year sampling dates were expected; however, the data do not support this hypothesis. Mean similarity for paired census dates was only 0.519 (*SD* = 0.196, range 0.204–0.854). Mean similarity was highest (0.593 [*SD* =

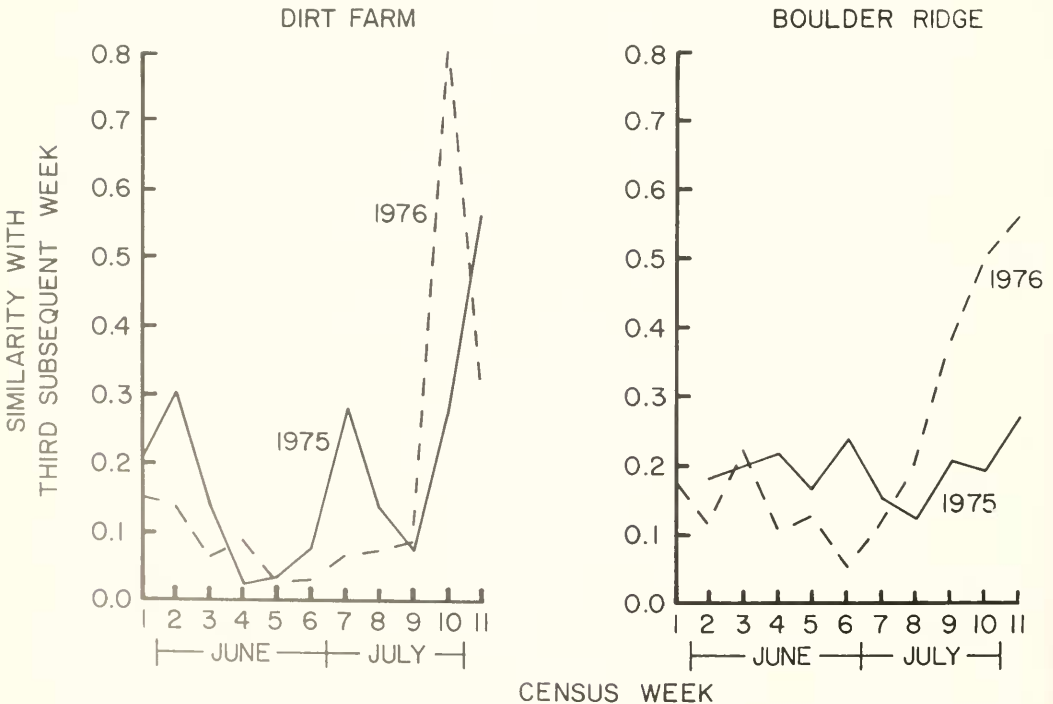


Fig. 5. Czekanowski similarity measures between floral abundance for each census date and the third subsequent week at both sites. Census date numbers refer to Table 1.

0.149, range = 0.265–0.772]) when each 1975 date was compared with the week prior to that date in 1976. Thus, the similarity data provide additional evidence for phenological advancement in 1976.

Within-year similarity comparisons were also quite variable. We reasoned that, since bees are the predominant pollinators on shortgrass prairie and because females of most species of solitary bees fly for a minimum of four weeks (Linsley 1958), a conservative estimate of within-year resource variability for a bee would be the similarity between the week of emergence and three weeks later. This measure is conservative because we used similarity measures between dates that are one week less than the minimum flight span. In Figure 5 we graph the results for each year. Except for the last month of the census period, values are very low. Any species emerging during the first two-thirds of the blooming season would face a very different flora during the latter part of its flight season relative to that encountered initially.

Cluster analysis aids in depicting seasonal groupings and transitional periods within the blooming season (Fig. 6). The number of clus-

ters formed at a value of .50 differs between years as does the number of unclustered dates, suggesting that the "structure" of the blooming season may differ from year to year. For example, five clusters plus one unclustered date form in 1975, but four clusters and four unclustered dates form in 1976.

Within both years late season dates cluster strongly, again indicating higher within-year predictability for late summer bees. Almost all other clusters are composed of only two consecutive census dates, indicating a high rate of turnover in floral composition for the first two-thirds of the blooming season.

Boulder Ridge

Phenology.—Flowering also began earlier in 1976 at Boulder Ridge (Fig. 7). Of the 73 species censused, 33 were either in bloom when censusing began or flowered in only one year and were eliminated from this analysis. Of the remaining 40 species, 32 showed phenological differences of at least one week. Twenty-six of the 32 species were earlier an average of 10 days in 1976 ($X^2 = 12.50$, $P < 0.001$). The seasonal differences in advancement between first- and second-half

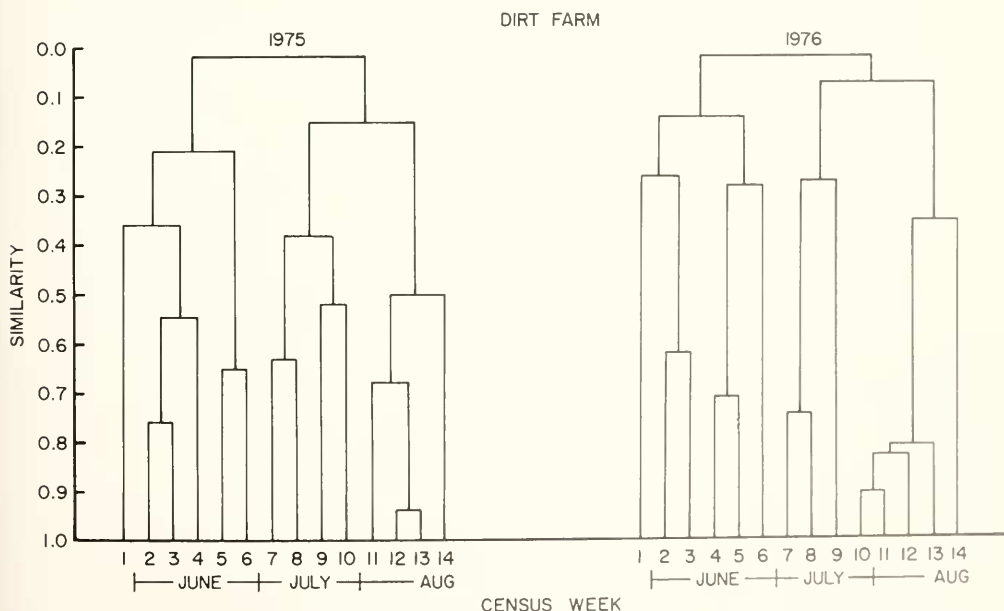


Fig. 6. Dendrograms of floral similarity between census dates for each year at The Dirt Farm. Census date numbers refer to Table 1.

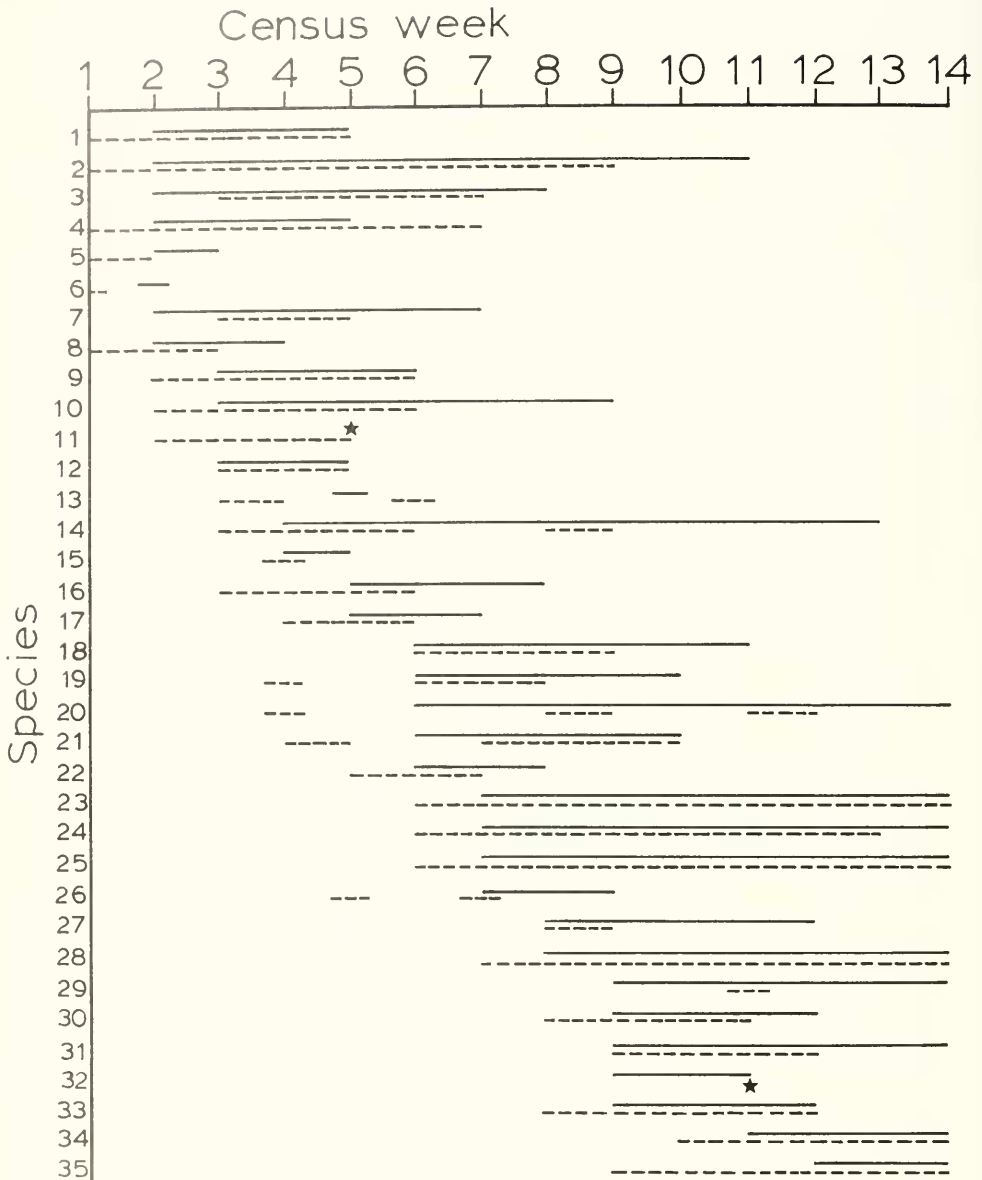


Fig. 7. Bloom spans of selected species at Boulder Ridge for 1975 (solid) and 1976 (dashed); stars = did not flower. Census date numbers refer to Table 1, species numbers to Appendix A.

species observed at The Dirt Farm were not detected here.

Most species differed in bloom span between years. After eliminating species that began blooming prior to censusing, 29 of the remaining 40 differed by at least one week. Average difference in bloom span for the 29 species was 17 days with a range of one to

five weeks. Chi-square analyses for seasonal patterns were insignificant. Year effects, however, were present; longer bloom spans were concentrated in 1975 (20 of 29, $X^2 = 4.17, P < 0.05$).

Abundance.—Differences in total floral abundance between years were remarkable (Fig. 8). Twelve of the 13 comparisons

showed significantly greater abundance in 1975. There was a marked midyear peak in 1975 that is only suggested in 1976.

In contrast to The Dirt Farm, floral abundance for all vegetation types at Boulder Ridge was higher in 1975 (Fig. 8). Between-year differences on the heterogeneous area were primarily responsible for the total flower differences. The last 10 dates showed significantly more flowers on this section in 1975 (Fig. 8). The second peak in the total abundance curve in 1975 (Fig. 8), absent in

1976, was due mainly to the heterogeneous area. Differences observed on the other sections showed floral abundances in 1976 to be consistently below those of 1975, although many of these comparisons were not significant.

The *RHL* ratio was used to compare abundance by species between years. We eliminated all species with less than 50 flowers in either years and those that flowered in only one year. For the remaining 38 species, mean $RHL = 5.47$ ($SD = 6.56$, range =

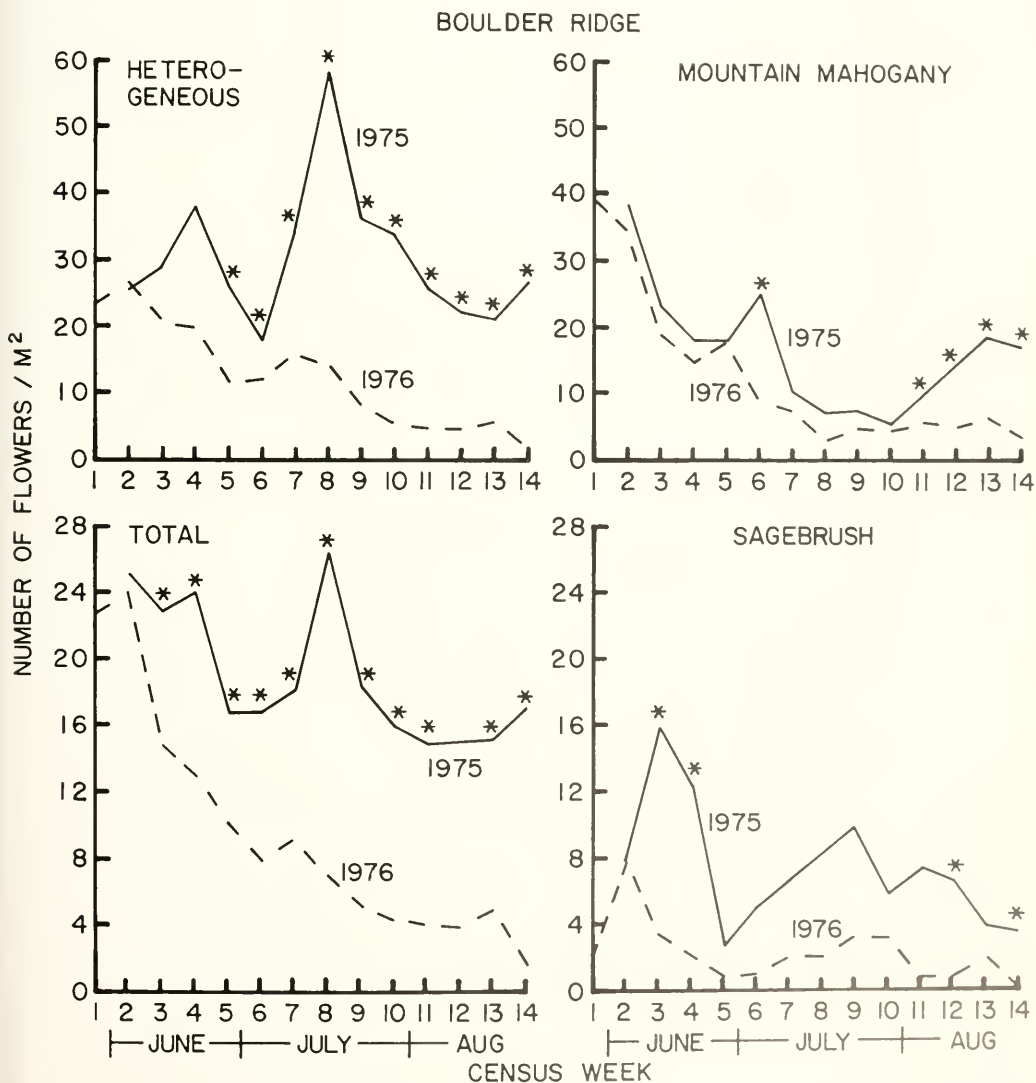


Fig. 8. Total abundance per m², irrespective of species, at Boulder Ridge for each census date in 1975 and 1976. Census date numbers refer to Table 1. Asterisks mark significant differences ($P \leq .05$ between years for paired dates).

1.07–27.50; Fig. 4). Again, there were large between-year differences in abundance for most species on the site.

We tested for seasonal differences in *RHL* values using the same methods as for The Dirt Farm. Again, *RHL* values for the latter part of the blooming season are significantly higher ($P < 0.05$). However, in contrast to The Dirt Farm, each year is not equally represented by species with high *RHL* values. Twenty-eight of the 38 species were more abundant in 1975 ($X^2 = 8.53, P < 0.005$). This phenomenon is particularly striking for the latter part of the blooming season, when only one of 16 species was more abundant in 1976.

Similarity and Cluster Analysis.—As with The Dirt Farm data, the expected high similarity for paired between-year comparisons was not evident. Mean similarity for paired census dates was only 0.424 ($SD = 0.200$, range = 0.184–0.896). Again, highest mean similarity was between 1975 dates and the week prior to the identical date in 1976 ($\bar{x} = 0.518, SD = 0.161$, range = 0.309–0.869).

Within-year similarities [between each census date and the census taken three weeks later] were as low as at The Dirt Farm (Fig. 5). The graph for 1975 is uniformly low without the appreciable rise late in the season

present in The Dirt Farm and Boulder Ridge 1976 data.

Cluster analysis again suggests “structural” differences between the blooming seasons (Fig. 9). Four clusters plus three unclustered dates form in 1975, and five clusters and three unaffiliated dates are found in 1976. As at The Dirt Farm, late season dates cluster most densely and all but one other cluster is composed of only two consecutive dates at the .50 level.

DISCUSSION

Plant species varied substantially between years in the onset and length of the blooming period and in the number of flowers produced. Comparison of phenology and abundance, both between sites and among vegetation types within sites, shows other important differences. Though phenological advancement in 1976 was a uniform occurrence at both sites, changes in the direction and magnitude of floral abundance were not. A comparison of total floral abundance between The Dirt Farm and Boulder Ridge shows that the two sites behaved quite differently. Floral production at Boulder Ridge in 1976 was consistently well below that of 1975. In con-

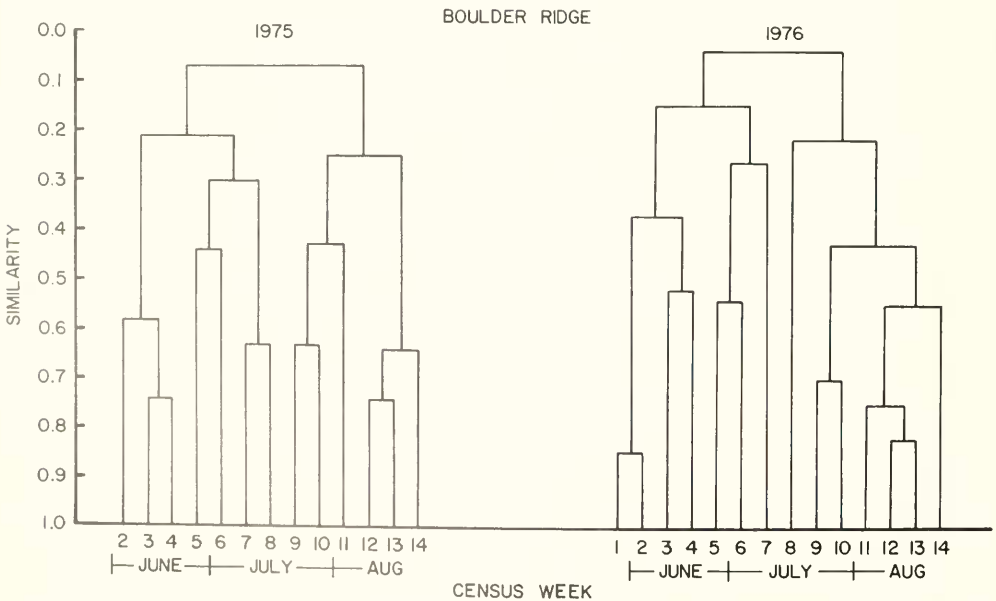


Fig. 9. Dendrograms of floral similarity between census dates for each year at Boulder Ridge. Census date numbers refer to Table 1.

trast, floral production was significantly higher at The Dirt Farm in 1976 over the latter part of the blooming season. Evidently, the spring and early summer drought was either more severe at Boulder Ridge or the plant communities at Boulder Ridge were more susceptible than those at The Dirt Farm.

Between-site differences appear due to varying responses to weather by each vegetation type within each site. At Boulder Ridge all communities displayed consistently lower floral productivity in 1976, but at The Dirt Farm each community responded independently. Indeed, at The Dirt Farm each species seemed to display an independent response as shown by the lack of any year effects on the distribution of *RHL* values either in between-year comparisons or between-season comparisons. These observations suggest that variation in floral production is expressed as spatially localized patches of high or low abundance that change from year to year.

Because we collected data for only two years, it is necessary to ask how representative of routine variability these results are. Schemske et al. (1978), in a study of seven spring herbs, found the onset of flowering to range, by species, from 8 to 22 days over three years. More importantly, peak flowering did not usually coincide with optimal pollinator conditions. Long-term bloom records for several regions in North America are available for analysis. In several cases data are available for period of up to 30 years in the same area (Lindsey and Newman 1956—Indiana; Smith 1915—Ohio; Hulbert 1963—Kansas; Hodson 1971—Minnesota). In examining these data we have used variability in first flowering as an indication of resource predictability since this phenophase is common to all studies. In brief, we find that almost all variability in the date of first bloom is accounted for with 10 years of observations and that the range of first bloom is between four and five weeks for most species (Tepedino and Stanton, unpublished manuscript). Other support for phenological variability exists. Recently West and Gasto (1978) reported that the onset of bloom of two arid land shrubs in northwestern Utah varied over seven years by 44 and 39 days. Thus, the substantial phenological variability recorded in

our study over two years is low relative to what can be expected over a 10-year period.

Long-term studies of floral abundance are few. Tamm (1948, 1956, 1972a, b) counted flowers of several species in permanent quadrats in forest and meadow in mid-Sweden for 14 to 29 years. All species showed large irregularities in year-to-year floral abundances from no flowers in some years to profuse abundance in others.

Short-term studies are more numerous. Ackerman and Bamberg (1974) reported large variation in floral abundance over a three-year period for *Lycium andersonii* in Nevada. Bykov (1974), in a general review of vegetation dynamics of the arid Turanian Plain, reported wide variation in floral abundance of both ephemerals and perennials. Sarukhan (1974) supplied floral abundance data for three species of *Ranunculus* for two years from permanent plots, with all species producing many more flowers in the first year. Holway and Ward (1965), studying the alpine plant community in northern Colorado over two years, noted that floral production in the second year was much lower. Davies (1976) used the same five trees of each of two species and recorded the number of individuals flowering over an eight-year period in western Australia. Combining data for both species (*Acacia pruinocarpa*, *Hakea lorea*; Davies 1976; Table 6) showed that in three of eight years the number of individuals flowering was 40 percent or less. Data on fruit crops also were presented for 10 species of shrubs and trees for 10 years. If we can assume that fruit crop bears at least a partial relation to floral production (Grubb 1977), floral production was irregular in 9 of the 10 species. Schemske (1977, 1978) has shown that the number of flowers of two woodland herbs censused in 78 permanent m² quadrats varied considerably between years. Moldenke (1976) noted that floral production varies widely between years in California grasslands. Treshow (1979), in a six-year study of the pinyon-juniper community in Utah, has shown that forb cover in almost every year differed significantly from each other year.

Year-to-year variation in floral abundance is not restricted to "unpredictable" temperate zone communities (Federov 1966). Mass flowering via synchronization of all members

of a particular species or many species in a community in the tropics at periodic intervals is well known (Whitmore 1975). Medway (1972) and McClure (1966) provided data showing widespread irregularity in flowering for 46 species of tropical rain forest trees in Malaya. Although most of the observations were recorded on very few individuals, it is enlightening to learn that the percent of species flowering each year ranged from 44 to 88 over the period from 1963 to 1968, with an average of 58 percent. Of 42 species observed for the entire six-year period, only 11 (26.2 percent) flowered every year, and 24 (57.1 percent) flowered in three or fewer years. In a study of flowering phenology in Ceylon, Koehneyer (1959) reported: "There was no regularity in the sequence of years of flowering and years in which there was no flowering in the individual trees. The result is the absence of a definite cycle of flowering."

The data seem clear. Where data on year-to-year floral abundances have been recorded, large variations in floral production are the rule rather than the exception.

Variability in floral resources may also be modified by seasonal influences. First, some parts of the blooming season may exhibit more year-to-year variability than others. Leopold and Jones (1947) hypothesized that early blooming species are more "turbulent" in first bloom than those which bloom later in the year. We reexamined the phenology data of Leopold and Jones (1947) for Wisconsin using multiple regression analysis and found that their Sauk County data do show a significant inverse correlation between range of first bloom and average first bloom date. Though the Dane County data show the same pattern, it is not significant (Tepedino and Stanton, unpublished manuscript).

The Wyoming data do not support the hypothesis of greater year-to-year "turbulence" in the spring flora. At The Dirt Farm, between-year differences in first bloom were significantly greater for plants that bloomed over the second half of the census period. At Boulder Ridge no significant difference between first- and second-half plant species was detectable. In addition, between-year differences in abundance (as judged by *RHL* ratios) were significantly greater for the last half of

the blooming season at both sites. Whether these differences were due to only two years' data from Wyoming or to conditions that are site specific is not clear.

The second way in which floral resources may vary seasonally is in predictability of subsequent resource abundance and composition. From this perspective the spring flora is, indeed, more turbulent; predictability, as judged by floral similarity values calculated at three-week intervals (Fig. 5), was low relative to average flight time for bees until the latter third of the bloom season when composites became dominant. This result may be somewhat misleading however, because more species begin bloom in spring than in late summer and low spring similarity values are due in large part to species additions.

Low year-to-year predictability in floral phenology and abundance must exert strong selection on flower-visiting insects. This is particularly true for bees because every stage in their life cycle is obligately dependent upon floral resources for food. When resources are unpredictable in time and/or space, selection should favor generalized consumers. Alternatively, specialization would require precise synchronization between bee emergence and anthesis of the host plant, particularly when the host has a brief bloom span. It is unclear how such precise synchronization might be affected. In most plant species studied photoperiodic stimuli initiate flower formation, but subsequent development and anthesis is profoundly modified by diverse factors such as moisture and nutrient availability and temperature (Evans 1969, Schwabe 1972). Our knowledge of the stimuli used by bees to cue emergence in a natural setting is scanty (Linsley 1958), but in the laboratory temperature alone is a reliable stimulus for several species (*Megachile rotundata* (Fabricius), *Osmia lignaria* Say, *Hylaeus bisinuatus* Forster, *Nomia melanderi* Cockerell, and several others; G. E. Bohart, F. D. Parker, P. F. Torchio, pers. comm., pers. obs.). Thus, though anthesis is determined by a complex of factors, bee emergence may be primarily responsive to temperature. Because of these differences in potential stimuli used by the two groups, synchronization may be rare. In this regard, Linsley (1958) noted that

studies of oligolectic bees frequently reveal poor synchronization.

Even if specialized bees could achieve close synchronization with host plant anthesis, the problem of year-to-year variation in resource quantity still remains. Attempting to track specific floral resources that vary widely could cause large fluctuations in the populations of bee specialists, thereby increasing the probability of local extinction (Tepedino 1979). The frequently expressed view that most temperate bees are specialized (van der Pijl 1966, Faegri and van der Pijl 1971, Heinrich 1976, Raw 1976, Heithaus 1979) will probably require modification because such specialization seems in-

consistent with documented fluctuations in floral resources.

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APPENDIX A. The number of flowers recorded in permanent m² quadrats at The Dirt Farm and Boulder Ridge in 1975 and 1976. Nomenclature: Harrington (1954), Weber (1967), Porter (1965). Numbers in the far left column refer to Figures 2, 7; the first number to Figure 2 (Dirt Farm), the second to Figure 7 (Boulder Ridge). A zero signifies nonrepresentation.

Species		Dirt Farm		Boulder Ridge	
		1975	1976	1975	1976
(0, 8)	Berberidaceae <i>Berberis repens</i> Lindl.	—	—	52	68
(19, 0)	Boraginaceae <i>Cryptantha flavoculata</i> (A. Nels.)	575	60	—	32
(23, 0)	<i>Cynoglossum officinalis</i> L.	50	47	—	—
(14, 0)	<i>Hackelia floribunda</i> (Lehm.)	67	109	—	—
(10, 0)	<i>Lappula vedowskii</i> (Hornem.)	—	—	5	2
(0, 5)	<i>Lithospermum incisum</i> Lehm.	133	16	9	9
	<i>Mertensia humilis</i> Rydb.	12	5	16	42
	Cactaceae <i>Opuntia polyacantha</i> Haw.	—	1	—	—
(38, 0)	Capparidaceae <i>Cleome serrulata</i> Pursh	5	101	—	—
(0, 23)	Caryophyllaceae <i>Arenaria fendleri</i> A. Gray	—	—	122	58
(24, 19)	<i>Arenaria hookeri</i> Nutt.	1165	625	1577	474
(0, 3)	<i>Cerastium arvense</i> L.	—	—	332	50
(22, 20)	<i>Paronychia sessiliflora</i> Nutt.	3489	3000	715	40
	<i>Stellaria media</i> (L.)	—	—	9	—
	Compositae <i>Achillea millefolium</i> L.	—	—	382	19
	<i>Antennaria microphylla</i> Rydb.	—	—	3343	959
	<i>Antennaria rosea</i> Greene	—	—	83	—
	<i>Artemisia frigida</i> Willd.	311	114	393	—
(40, 34)	<i>Aster rubrotinctus</i> Blake	393	73	87	15
(35, 28)	<i>Chrysopsis villosa</i> (Pursh)	262	116	2426	676
(39, 0)	<i>Chrysothamnus nauseosus</i> (Pallas)	1882	73	—	—
(42, 0)	<i>Chrysothamnus viscidiflorus</i> (Hook.)	1906	4216	11	3
	<i>Cirsium undulatum</i> (Nutt.)	17	4	2	—
(0, 24)	<i>Erigeron canus</i> A. Gray	—	2	817	314

Appendix A continued.

Species		Dirt Farm		Boulder Ridge	
		1975	1976	1975	1976
12, 2	<i>Erigeron nematophyllus</i> Rydb.	434	406	895	1014
	<i>Erigeron pumilus</i> Nutt.	59	—	12	—
41, 35	<i>Gaillardia aristata</i> Pursh	—	—	7	—
	<i>Gutierrezia sarothrae</i> (Pursh)	2163	3170	1512	735
	<i>Haplopappus nuttallii</i> T. & G.	—	45	—	—
34, 29	<i>Helianthella uniflora</i> (Nutt.)	45	35	50	3
30, 14	<i>Hymenoxys acaulis</i> (Pursh)	62	81	82	24
6, 0	<i>Hymenoxys torreyana</i> (Nutt.)	342	248	—	—
13, 9	<i>Senecio canus</i> Hook.	499	701	21	53
	<i>Senecio integerrimus</i> Nutt.	10	11	—	19
0, 30	<i>Solidago spathulata</i> DC	—	—	227	100
	<i>Taraxicum</i> sp. Hall	—	—	57	—
	<i>Townsendia sericea</i> Hook.	4	—	2	—
Crassulaceae					
0, 18	<i>Sedum stenopetalum</i> Pursh	—	—	1768	535
Cruciferae					
4, 0	<i>Arabis fendleri</i> (Wats.)	89	166	—	—
	<i>Arabis holboellii</i> Hornem.	—	—	13	17
21, 0	<i>Descourainia sophia</i> L.	128	225	—	—
	<i>Draba nemorosa</i> L.	—	35	581	207
15, 11	<i>Erysimum capitatum</i> (Dougl.)	—	122	—	160
	<i>Halimolobos virgata</i> (Nutt.)	12	—	—	—
8, 10	<i>Lesquerella ludoviciana</i> (Nutt.)	1839	332	466	360
0, 7	<i>Physaria australis</i> (Payson)	48	—	219	84
17, 0	<i>Sisymbrium altissimum</i> L.	24	52	—	—
	<i>Sisymbrium lineifolium</i> Nutt.	27	—	—	—
Euphorbiaceae					
	<i>Euphorbia</i> sp. L.	279	325	366	187
Gentianaceae					
	<i>Succria radiata</i> (Kellogg)	—	—	1	6
Labiatae					
32, 0	<i>Hedeoma drummondii</i> Benth.	971	75	—	—
	<i>Scutellaria brittonii</i> Porter	—	9	—	—
Leguminosae					
25, 0	<i>Astragalus bisulcatus</i> Hook.	125	88	—	—
	<i>Astragalus crassicaerpus</i> Nutt.	9	2	—	—
0, 21	<i>Astragalus flexuosus</i> Dougl.	—	—	438	31
9, 0	<i>Astragalus sericoleucus</i> Gray	21	57	—	—
	<i>Astragalus shortianus</i> Nutt.	—	—	18	—
7, 0	<i>Astragalus spatulatus</i> Sheld.	386	329	—	—
0, 32	<i>Astragalus striatus</i> Nutt.	—	—	41	—
0, 12	<i>Thermopsis rhombifolia</i> Nutt.	—	—	84	43
Liliaceae					
37, 31	<i>Allium cernuum</i> Roth	1771	2693	478	98
0, 16	<i>Allium geyeri</i> Wats.	—	—	853	607
15, 17	<i>Allium textile</i> Nels. & Macbr.	622	1284	187	200
	<i>Calochortus nuttallii</i> Torrey	1	—	—	—
0, 1	<i>Leucocrinum montanum</i> Nutt.	—	—	73	122
11, 0	<i>Zygadenus venenosus</i> Wats.	211	314	—	—
Linaceae					
	<i>Linum lewisii</i> Pursh	—	25	17	2

Appendix A continued.

Species		Dirt Farm		Boulder Ridge	
		1975	1976	1975	1976
Malvaceae					
	<i>Sphaeralcea coccinea</i> (Pursh)	28	—	—	—
Onagraceae					
(31, 0)	<i>Gaura coccinea</i> Nutt.	317	67	—	—
	<i>Oenothera coronopifolia</i> T. & G.	—	—	1	—
Polemoniaceae					
	<i>Gilia spicata</i> Nutt.	—	—	—	7
	<i>Microsteris humilis</i> (Dougl.)	—	—	4	—
(1, 0)	<i>Phlox bryoides</i> Nutt.	6511	7526	—	—
(2, 6)	<i>Phlox hoodii</i> Rich.	91	42	12	85
Polygonaceae					
	<i>Eriogonum alatum</i> Torr.	41	—	192	—
(36, 0)	<i>Eriogonum effusum</i> Nutt.	28,869	57,115	—	—
(0, 33)	<i>Eriogonum jamesii</i> Benth.	—	—	84	298
(28, 22)	<i>Eriogonum umbellatum</i> Torr.	852	284	282	73
Portulacaceae					
	<i>Claytonia lanceolata</i> Pursh	—	—	4	19
Primulaceae					
	<i>Androsace septentrionalis</i> L.	—	—	27	22
Ranunculaceae					
(26, 0)	<i>Delphinium nelsoni</i> Greene	11	56	13	14
(0, 4)	<i>Ranunculus ranunculinus</i> (Nutt.)	—	—	4284	5509
Rosaceae					
(0, 15)	<i>Amelanchier alnifolia</i> Nutt.	—	—	220	8 ^a
(16, 13)	<i>Cercocarpus montanus</i> Raf.	8047	3752	128	219
	<i>Potentilla concinna</i> Richards	—	—	9	1
	<i>Potentilla fissa</i> Nutt.	—	—	6	2
(29, 0)	<i>Potentilla hippiana</i> Lehm.	862	375	20	3
Santalaceae					
	<i>Commandra umbellata</i> (L.)	243	5	14	98
Saxifragaceae					
	<i>Ribes cereum</i> Dougl.	—	—	3	7
Scrophulariaceae					
(0, 25)	<i>Castilleja flava</i> Watson	—	—	912	361
	<i>Collinsia parviflora</i> Dougl.	—	—	565	402
	<i>Othocarpus luteus</i> Nutt.	—	—	571	323
(20, 0)	<i>Penstemon angustifolius</i> Nutt.	67	84	—	—
(27, 0)	<i>Penstemon ciantherus</i> Pursh	61	12	4	1
(33, 27)	<i>Penstemon laricifolius exilifolius</i> (A. Nels.)	449	220	966	83
(0, 26)	<i>Penstemon strictus</i> Benth.	—	—	44	7
Umbelliferae					
(5, 0)	<i>Harbouria trachypleura</i> (A. Gray)	667	196	—	8
Violaceae					
(3, 0)	<i>Viola nuttallii</i> Pursh	73	52	—	4
Species total		56	55	57	60
Totals (both years)		63		73	

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